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The effects of temperature on the intensive production of *Lumbricus terrestris* (Oligochaeta: Lumbricidae)

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With 2 figures

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1. Introduction

A growing number of studies have revealed that earthworms are capable of improving the fertility and productivity of reclaimed soils (e.g. STOCKDILL, 1982; HOGERKAMP *et al.*, 1983; CURRY, 1988). There is, therefore, a potential demand from local authorities, land owners and particularly mineral companies for large numbers of earthworms to accelerate soil amelioration as part of land restoration work (CURRY & COTTON, 1983; BRUN *et al.*, 1987). At present this demand for earthworms could only be partially met by labour intensive, field collection techniques of the types described by RAW (1959) or TOMLIN (1983). However, an alternative supply could possibly be produced under intensive conditions. Experience gained with *Eisenia fetida* (e.g. HARTENSTEIN *et al.*, 1979) showed that litter-dwelling earthworms could easily be produced but similar production of larger, deep burrowing earthworms was uncertain. During a research programme, to investigate the possible intensive production of *Lumbricus terrestris* for soil amelioration (BUTT, 1990), the influence of temperature, a vital parameter, was examined. The effects of temperature on the life cycle of many earthworm species are widely reported (EVANS & GUILD, 1948; GERARD, 1960; NOWAK, 1975; PHILLIPSON & BOLTON, 1977; TSUKAMOTO & WATANABE, 1977; NEUHAUSER *et al.*, 1979; REINECKE & KRIEL, 1981; LOFS-HOLMIN, 1983). These and other authors have shown that each earthworm life stage, (cocoon production, cocoon development and hatching growth) may be influenced by environmental temperature.

LEE (1985) reports thermal optima in the temperature range of 10–15 °C for natural populations of Lumbricidae in Europe. DAUGBJERG (1988), assessed moisture and temperature preferences of several earthworm species in the laboratory and found a stenothermal preference of 10 °C for *L. terrestris*. Most laboratory work with this species had been conducted at temperatures around 15 °C, although TOMLIN (1977) considered 11–13 °C to be a high temperature at which to keep this earthworm. Since the pioneering work of EVANS & GUILD (1948) few workers, with the notable exceptions of MEINHARDT (1974), LOFS-HOLMIN (1983) and HARTENSTEIN & AMICO (1983), have investigated and manipulated the growth and reproductive biology of *L. terrestris*. This dearth of research is almost certainly due to the low reproductive potential of this species compared with other earthworms.

L. terrestris is an obligate biparental earthworm (EVANS & GUILD, 1947; MICHON, 1954). Mating takes place on the soil surface and cocoons are produced at approximately ten day intervals, their development taking twelve to thirteen weeks (MEINHARDT, 1974). In Britain, natural growth to maturity is usually attained within one year, (EVANS & GUILD, 1948; LAKHANI & SATCHELL, 1970), but in Scandinavia this may take fifteen months (NORDSTRÖM, 1976). SATCHELL (1967) suggests that *L. terrestris* mating will occur throughout the year, except when soil conditions are unsuitable. GATES (1961) reports that this species has been found in reproductive condition from March to December.

2. Materials and methods

The soil used throughout this work was a loamy sand (Anonymous, 1984) with 50–70% sand and 15% clay. It was rough and gritty with a total ash content of $880 \text{ g} \cdot \text{kg}^{-1}$ and a pH of 7.5. Before use the soil was sieved through a 12 mm mesh and steam sterilised to remove potential predators and any living earthworm material.

The two feeds used, separated cattle solids and paper pulp, were obtained from AFRC Engineering, Silsoe, and U.K. Paper, Sittingbourne, respectively. Before use the cattle solids were dried to remove excess ammonia and then rewetted. A full description of each feed is provided in table 1.

2.1. Cocoon production

An experiment designed to examine the effects of temperature on cocoon production over a twelve month period was begun in August 1988. Healthy, mature *L. terrestris* L. were obtained from the grounds of the Open University, by the formalin expellent method (RAW 1959), and maintained in darkness, under controlled or semi-controlled temperature environments. Three temperature regimes were chosen for examination. These were; (a) constant 15°C (incubator), (b) higher fluctuating (indoor store) and (c) low fluctuating (outdoor store). Both (b) and (c) had air temperature fluctuations recorded as monthly maximum and minimum values. From these readings, mid-range values were calculated. These proved to be closest to recorded soil temperatures within the experimental vessels, obtained periodically, using an automatic temperature recorder. The constant temperature of 15°C was chosen as it was known to be within the optimum range suggested by previous workers (LOFS-HOLMIN, 1985).

Table 1. Feed characteristics.

Feed	% Total Solids	Neutral Det. Fibre (%)	Acid Det. Fibre (%)	Hemi-cellulose (NDF-ADF)	Cellulose (%)	Lignin (%)	Ash (%)	Total Kjel. Nitrogen (%)	Total Carbon (%)	C:N	pH
Separated Cattle solids	27.1	72.4	54.1	18.3	15.7	13.4	25.0	2.0	31.5	16:1	9.1
Paper pulp	19.6	84.1	72.1	11.9	49.1	12.0	10.2	0.5	46.7	93:1	7.1

Ninety clitellate worms were selected and divided into eighteen groups of five. These were weighed (mean individual earthworm mass 5.3 g) and each group was placed in a 2.5 litre vessel (height 18 cm) containing two litres of moistened sterilised soil with a surface supply of excess dried, crumbled and rewetted separated cattle solids, a proven feed from earlier trials (BUTT, 1990). Six vessels were randomly allocated to each temperature regime. Checks on feed supply and soil moisture content (maintained at 25–30%) were made every two weeks by visual inspection and air drying, of a small weighed soil sample from a limited number of vessels, respectively. Sampling occurred at the start of each calendar month, the soil was removed from each vessel and wet-sieved through mesh sizes (6.7, 3.35 and 2 mm) to obtain cocoons. The worms were counted, weighed, and examined for sexual and general condition and then returned to the vessels, which were resupplied with fresh soil and feed. An analysis of variance was applied to the data to investigate the effects of the different temperature regimes on cocoon production.

2.2. Cocoon incubation

Cocoons were collected at fourteen day intervals from soil, in which field-collected, reproductively active worms had been maintained at 15°C . Each cocoon was washed, dried, weighed and placed individually on a filter paper in a petri dish half filled with water. These petri dishes were assigned in rotation to constant temperature incubators at either 5, 10, 15, 20 or $25 \pm 1^\circ\text{C}$. Daily inspections were made of the 575 cocoons collected, to record hatching or the need for replenishment of water. On hatching the length of the incubation period was recorded, the hatchlings were weighed and retained for use in growth experiments. The total incubation duration was determined by the addition of seven

days to the cocoon incubation period. Any cocoons which failed to hatch were dissected when the elapsed incubation period was greater than twice the mean value then known for that particular temperature. The effect of temperature on successful development (hatchability) could then be calculated. A further fifty cocoons were individually frozen on collection, in order to assess their subsequent viability. After a period of several weeks these were defrosted and ten were kept at each of the above constant temperatures.

2.3. Hatchling growth and survival

Initially all hatchlings used in this experiment were obtained from cocoons which had developed at a temperature of 15 °C. Individual hatchlings were placed in 300 ml plastic pots containing 200 g of moist sterilised soil and 50 g of paper pulp as feed. Promising growth results had been obtained using this feed in earlier work (BUTT, 1990). The pots were assigned, on a rotational basis, to one of five constant temperatures, at five degree intervals, in the range 5–25 °C. Worms were weighed monthly, at which time soil and feed were replaced. These experiments were monitored for a minimum of twenty weeks, when levels of survival were recorded.

On completion of an experiment to examine the effect of temperature on cocoon incubation duration (section 2.2) the hatchlings obtained were treated as above but a record of their incubation temperature was also noted. This allowed a comparison to be made between growth rates at a range of constant temperatures following incubation at a similar range of constant temperatures, i.e. it permitted an investigation into the possible effect of incubation temperature on subsequent growth. Hatchlings from cocoons incubated at 10, 15 and 20 °C were grown at 10, 15, and 20 °C; all nine combinations were examined. Neither growth at a higher temperature following incubation at 5 °C, nor growth at lower temperatures following incubation at 25 °C was examined, due to the length of the incubation period and low viability of incubated cocoons, respectively.

3 Results

3.1. Cocoon production

Figure 1 shows cumulative cocoon production and a representation of recorded temperatures at each of the three temperature regimes over a complete twelve month period. An analysis of variance revealed that the temperature regimes had a significant effect ($p < 0.001$) on annual cocoon production.

At a constant 15 °C (fig. 1a) mean cocoon production was 25.3 cocoons per worm per year. The production rate rose from 1.9 cocoons per month during August and remained relatively constant at 2.8 cocoons per month from November to May; however, by July this figure had dropped to 0.9. After twelve months sixty-eight per cent of the adult worms had survived and all were fully clitellate (mean mass 4.2 g). At the higher fluctuating

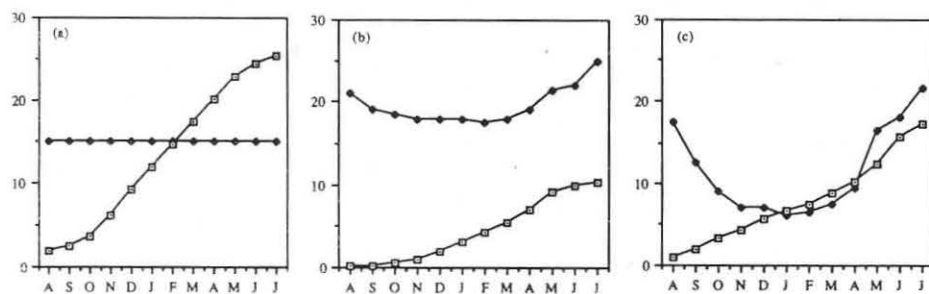


Fig. 1. Cumulative cocoon production by *L. terrestris* (1988/9) under 3 temperature regimes: (a) constant 15 °C, (b) Higher fluctuating, (c) Lower fluctuating. (□) Cocoon production, (◆) Temperature (°C).

temperature regime ($20 \pm 2^\circ\text{C}$ for ten months; fig. 1b) mean cocoon production was 10.1 cocoons per worm per year. An increased rate of production was recorded from March to May, at 1.9 cocoons per month, as the temperature rose from 18 to 21°C . Monthly cocoon production then fell below unity as the temperature reached 22°C . Forty per cent of the worms remained alive after one year, but of those only seventy-five per cent were clitellate (mean mass 3.6 g). At lower fluctuating temperatures, where a large variation was recorded, (fig. 1c) mean cocoon production was 17.2 cocoons per worm per year. An increased rate of production, at 2.1 cocoons per month, was recorded from February to June as the temperature rose from 6 to 18°C . However, the following month when the temperature rose above 20°C cocoon production was halved. After twelve months of monitoring, eighty-six per cent of the worms had survived; all were clitellate, with a mean mass of 5.5 g. Only under regimes (a) and (c) were cocoons produced during each of the monitored months.

3.2. Cocoon incubation

Incubation at a range of constant temperatures had a significant effect on cocoon development ($p < 0.05$). Development was most rapid at a temperature of 20°C , when a mean incubation duration of 70 ± 2.9 days was required (table 2). Below 20°C incubation duration steadily increased and reached approximately nine months at 5°C . Cocoon viability was close to seventy per cent at each constant temperature examined in the range $5-20^\circ\text{C}$, but was greatly reduced to forty-one per cent at a temperature of 25°C . At this higher temperature development within the cocoon lasted 81 days.

Table 2. Effects of constant temperatures on cocoon incubation duration and success, plus hatchling survival and mean mass after twenty weeks.

Temperature ($^\circ\text{C}$)	5	10	15	20	25
Incubation duration (days)	272 (a)	183 (b)	90 (c)	70 (d)	81 (e)
Hatchability (%)	66	72	71	74	41
Hatchling survival (%)	100	98	96	87	11
Mean mass (g)	0.29	0.53	1.50	3.10	—

Means followed by the same letter are not significantly different ($p > 0.05$).

Cocoons that had been frozen and subsequently defrosted failed to hatch at all five incubation temperatures. Inspection of their contents revealed no evidence of embryonic development.

3.3. Hatchling growth and survival

Figure 2 shows the influence of different temperatures on hatchling growth. Higher temperatures, in the range 5 to 20°C , led to increased growth rates. At 25°C , growth to four weeks was similar to that at 20°C but thereafter, high mortality and mass loss prior to death was recorded. Survival of hatchlings was considered of equal importance to recorded growth rates (table 2). A higher temperature within the range of 5 to 20°C led to only a small decrease in survivorship, only at 25°C was survivorship low. At 20°C both rapid growth ($20-30 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) and a high level of survivorship (87%) were recorded.

At temperatures of 10 , 15 and 20°C , hatchlings showed temperature related growth regardless of the temperature at which they had developed as cocoons. Hatchling growth curves from cocoons incubated at known temperatures were not dissimilar to those described in figure 2, where less control over incubation temperature had occurred.

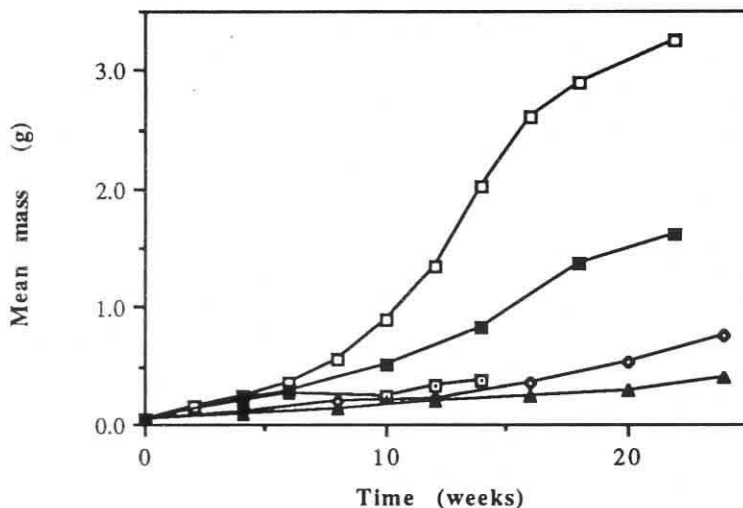


Fig. 2. Mean hatchling growth of *L. terrestris* at a range of constant temperatures ($n = 8$). (▲ 5 °C, ✕ 10 °C, ■ 15 °C, □ 20 °C, ◇ 25 °C).

4. Discussion

4.1. Cocoon production

As demonstrated by previous authors (e.g. PHILLIPSON & BOLTON, 1977; REINECKE & KRIEL, 1981) cocoon production can be influenced by environmental temperature. The mean cocoon production of one every 14.4 days at a constant 15 °C was less than that given by MEINHARDT (1974), — one every 10 days — but the latter was only recorded over a short period of time and therefore did not take into account any seasonal variation.

Physiological and behavioural responses almost certainly led to lower cocoon production under the two fluctuating temperatures regimes, compared with constant temperature conditions. FITZPATRICK *et al.* (1987), demonstrated that mature earthworms [*L. terrestris*] cultured at 10 and 15 °C were considerably more robust than those maintained at either 5 or 20 °C, particularly after a period of several weeks. However, changing temperatures in the experiments described here, particularly an increase in the range 10–20 °C led to increased cocoon production. EVANS & GUILD (1948) reported a similar trend in cocoon production for *L. rubellus*, when a four fold increase was recorded as the temperature increased in the range 6–16 °C. This type of response, also shown by *Aporrectodea rosea* (PHILLIPSON & BOLTON, 1977), may in part, account for the observed seasonal cocoon production of many European earthworm species reported to be greatest during the spring months (SATCHELL, 1967).

Lengthy exposure to temperatures above 15 °C led to what EVANS & GUILD (1948) termed fatigue. This could result directly from experience of higher temperatures or be a function of reproductive exhaustion. Neither the presence of excess food, nor acceptable moisture levels were sufficient to compensate for reduced cocoon production. After exposure to temperatures greater than 20 °C, at which FITZPATRICK *et al.* (1987) found *L. terrestris* to be least robust, many of the worms which had been in good general and reproductive condition, lost their clitellate appearance, lost mass and subsequently died. Unlike earthworms in natural environments, these experimental animals were unable to take refuge at greater, and hence cooler soil depths, a factor which almost certainly accounted for a high proportion of mortality. SATCHELL (1967) found that 50% of *L. terrestris* cultured in

the soil outside, survived to three years showing no sign of senescence. However in the current experiments the observed loss of reproductive condition may signal senescence and be a function of age rather than a reaction to temperature, as the age of these worms was unknown, and other species such as *E. fetida* (HARTENSTEIN *et al.*, 1979) are known to exhibit a decline in reproductive output after a given period. Further experiments using laboratory bred worms aim to assess this.

The earthworms maintained at a constant temperature exhibited uneven cocoon production throughout the year which could not be attributed to changes in temperature but was very similar to natural seasonal patterns. Either these worms were able to detect the seasonal changes, possibly through light breaks at sampling, or perhaps they were using some form of internal, biological clock.

4.2. Cocoon incubation

MEINHARDT (1974) reports that cocoon development of *L. terrestris* normally takes 12–13 weeks, but this time can vary, mainly in response to soil temperature. In these experiments the cocoon incubation duration was reduced to ten weeks, at 20 °C a temperature unlikely to be experienced in the soils of temperate regions (SACHELL, 1967) where cocoons are usually deposited at a depth of 0–10 cm (GERARD, 1964). A further increase in temperature, to 25 °C, led to an associated increase in mean development time, suggesting that a temperature close to 20 °C is optimal for this species. The death of all frozen cocoons was possibly due to ice crystal formation. Under natural conditions, cocoons would remain in a semi-dormant state at low temperatures, in order to over-winter, but would not be deposited so close to the soil surface that freezing would occur.

The marked decrease in cocoon viability for *L. terrestris* associated with an increase in incubation temperature at 25 °C was similar to the results obtained by TSUKAMOTO & WATANABE (1977) for *E. fetida*, where eighty-eight per cent hatched at 10 °C but less than forty-one per cent at 25 °C.

4.3. Hatchling growth and survival

At a temperature of 20 °C growth rates for *L. terrestris*, at 20–30 mg · g⁻¹ · d⁻¹ were only half of those obtained by HARTENSTEIN & AMICO (1983). However, both figures are much greater than any given for natural populations of this species. LAKHANI & SACHELL (1970) report rates of 10 mg · g⁻¹ · d⁻¹ in mineral soil under mixed woodland while CURRY (1988) gives 6.6 mg · g⁻¹ · d⁻¹ for growth in reclaimed peat grassland. Growth rate comparisons from different experiments must be made with caution as they are not constant throughout life even under ideal conditions. Further research has demonstrated that the growth rates obtained during the present experiments were limited by the nature of the feed provided (BUTT *et al.*, 1991).

Increased survival would be expected for laboratory reared worms compared to naturally existing populations, due to removal of environmental pressures such as predation. The twenty per cent mortality after 120 days, predicted by the model of LAKHANI & SACHELL (1970) for natural populations, was not reached during this work. Mortality over a similar period, for hatchlings fed paper pulp, at temperatures of 20 °C and below, was less than thirteen per cent. Mortality at 25 °C was thought to have been high (89%) because this temperature is close to 28 °C, the upper lethal limit for this species (WOLF, 1938).

As subsequent growth appeared to be unaffected by cocoon incubation temperature, a system for promoting maximum production of *L. terrestris* could focus on growth, rather than cocoon incubation temperature.

5. Conclusions

Temperature had a marked effect on all three phases of the *Lumbricus terrestris* life cycle. Under controlled laboratory conditions cocoon development was most rapid at 20 °C, cocoon viability was not reduced significantly and growth of hatchlings to maturity was also achieved in the shortest time. Survival of hatchlings to twenty weeks was also greater than eighty-seven per cent certain at this temperature. However, greatest annual cocoon production was recorded at a constant 15 °C. Fluctuating temperature regimes gave lower annual results, but production was enhanced during periods of increased environmental temperature, particularly in the range 10–20 °C. It has been demonstrated that *L. terrestris* can reproduce throughout the year, but seasonal production was seen to occur for this species even under constant temperature conditions.

To intensively produce *L. terrestris*, careful control of soil temperature must be maintained. This would permit manipulations in order to maximise successful, rapid cocoon development and hatchling growth whilst retaining a high level of cocoon production and overall worm survival. The reproductive phase of the life cycle appears to be particularly sensitive to temperature and may be the critical life cycle phase. It is suggested that an internally regulated mechanism may control reproductive timing.

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Laboratory based experiments were carried out to assess the effects of temperatures, in the range 0–25 °C, on intensive production of the earthworm *Lumbricus terrestris* L. Each phase of the life cycle was examined. Cocoon production of 25.3 cocoons, over a continuous twelve months, was greatest at a constant 15 °C compared with two fluctuating temperature regimes. Length of cocoon incubation was shortest at 20 °C, taking 70 days, with hatchability at 74%. With a feed of paper pulp, greatest hatchling growth rates of 20–30 mg · g⁻¹ · d⁻¹ were recorded at 20 °C. Hatchling mortality at twenty weeks was less than 13% at all temperatures tested below 25 °C. A temperature between 15 and 20 °C was concluded to be the most satisfactory for overall *L. terrestris* production.

Keywords: Temperature, *Lumbricus terrestris*, Intensive production, Life stages.

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